

Systematic palaeontology (Vertebrate palaeontology).

A new aspidorhynchid fish (Teleostei: Aspidorhynchiformes) from the Upper Jurassic of Ettling, Solnhofen, Bavaria, Germany

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Abstract

A new species of Aspidorhynchidae is described for the first time from the Late Jurassic of Ettling, some 50 km E-SE of Solnhofen, Bavaria, Germany. This new material is attributed to a new species, *Aspidorhynchus sanzenbacheri*, and is diagnosed by the abbreviated premaxillae, the form and disposition of teeth in the prementary, and the number of principal rays in the caudal fin.

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Résumé

Un nouveau poisson aspidorhynchidé (Teleostei : Aspidorhynchiformes) du Jurassique supérieur d'Ettling, Solnhofen, Bavière, Allemagne. Une nouvelle espèce d'Aspidorhynchidae est décrite pour la première fois du Jurassique supérieur d'Ettling, à 50 km à l'E-SE de Solnhofen (Bavière, Allemagne). Ce nouveau matériel est attribué à une nouvelle espèce, *Aspidorhynchus sanzenbacheri*, basée sur la faible longueur des prémaxillaires, la disposition des dents sur le prémentaire et le nombre de rayons composant la nageoire caudale. **Pour citer cet article :** P.M. Brito, M. Ebert, C. R. Palevol 8 (2009).

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Mots clés : Neopterygii; Aspidorhynchidae; Jurassique; Bavière; Allemagne

1. Introduction

The Aspidorhynchidae is a Mesozoic actinopterygian family, with a worldwide distribution, and confirmed temporal range from the Middle Jurassic to the Late Cretaceous [8].

Aspidorhynchids form a monophyletic assemblage of four nominal genera: *Aspidorhynchus*, *Belonostomus*, *Vinctifer*, and *Richmondichthys* although there is also an indeterminate taxon from the Cretaceous of Chile [4] that differs from the others by its toothless prementary and a somewhat square-shaped opercle.

Although the family Aspidorhynchidae was erected at the end of the 19th century [18], and several authors had studied the constituent taxa [1,5,8,12,16,21,28], the phylogenetic relationships of the Aspidorhynchidae within

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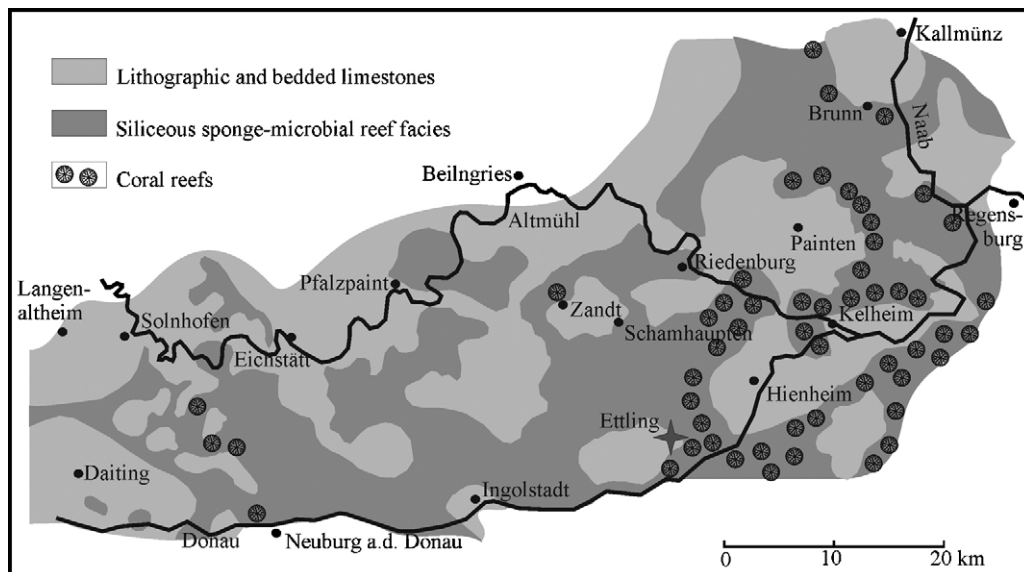


Fig. 1. Map of the Solnhofen area, southern Franconian Alb, Bavaria (modified after Röper et al. [20]).

Fig. 1. Carte de la région de Solnhofen, Bavière (modifiée d'après Röper et al. [20]).

the neopterygians are still in debate [2,8]. Some of this debate hinges on the difficulties in polarizing some of the anatomical complexes, especially in Jurassic members of the family, which have yet to be studied in detail. By contrast, Cretaceous taxa, especially the genus *Vinctifer* is by far the most well studied [7,8,10,16].

In the present work a new species of *Aspidorhynchus* from the Kimmeridgian/Tithonian of Ettlting in the Solnhofen area, southern Franconian Alb, Bavaria (Fig. 1), is described and comments regarding the nominal species of *Aspidorhynchus* are provided.

2. The species of *Aspidorhynchus*

There are seven Jurassic nominal species of *Aspidorhynchus* yet described, occurring in Germany, France, England, Cuba, and Antarctic [8]. The new species constitutes the eighth valid nominal species of the genus and the second species from the Jurassic of Bavaria.

The type species of the genus, *Aspidorhynchus acutirostris*, was described from the Tithonian of Solnhofen, Bavaria, for a large species, reaching a length of about 1 m total length [1]. This species had been previously described as *Esox acutirostris* [6], although this same species had been figured in 1775 [15]. *A. acutirostris* has been the subject of numerous studies, being reported with different specific names such as *A. longissimus* [17], *A. speciosus* [1], *A. mandibularis* [1,24], *A. ornatissimus* [1,26], or even

Belonostomus microcephalus [25]. *A. acutirostris* is also found in the Kimmeridgian of Cerin, France [21] in where it existed sympatrically with a second species of the genus, *A. sphekodes* [22]; this last species being distinguished from all other *Aspidorhynchus* species by the extremely elongated body.

Three species of *Aspidorhynchus* had been described from England: *A. euodus* [12], a moderate size species from the Callovian and Kimmeridgian, and two small species from the Purbeck group and the Bathonian, respectively: *A. fisheri* [13] and *A. crassus* [27], the earliest known aspidorhynchid.

Two species of *Aspidorhynchus* are known outside of Europe: *A. antarcticus* [19], based on an incomplete specimen preserving the postpelvic skeleton and one from Cuba, *A. arawaki* [8,9], a small size species differing from all other species by the length of its rostrum.

Aspidorhynchus was also reported in the Lower Cretaceous of Australia [14] although this occurrence, without any description or figures, requires confirmation.

3. Systematic paleontology

FAMILY Aspidorhynchidae Nicholson and Lydekker, 1889

GENUS *Aspidorhynchus* Agassiz, 1833

Type species: *Aspidorhynchus acutirostris* (Blainville, 1818).

Generic diagnosis: Brito [8].

ASPIDORHYNCHUS SANZENBACHERI sp. nov.

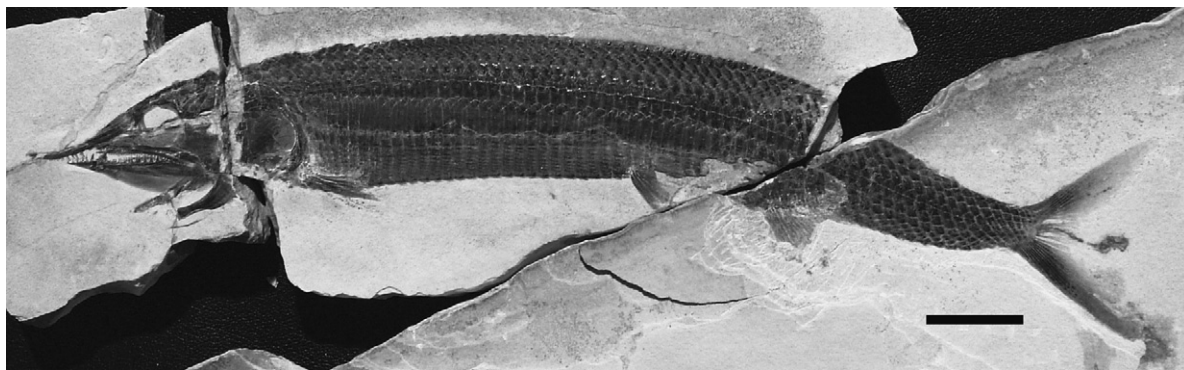


Fig. 2. *Aspidorhynchus sanzenbacheri* n. gen et sp.; holotype JME-ETT1 (scale: 5 cm).

Fig. 2. *Aspidorhynchus sanzenbacheri* n. gen et sp.; holotype JME-ETT1 (échelle : 5 cm).

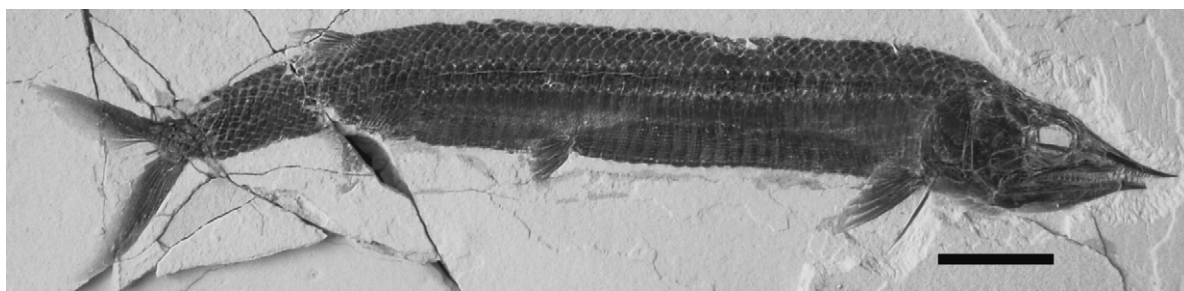


Fig. 3. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT2 (scale: 5 cm).

Fig. 3. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT2 (échelle : 5 cm).

Holotype: JME-ETT1: an almost complete specimen, Jura Museum, Eichstätt, Bavaria, Germany (Fig. 2).

Additional material: seven specimens from the Jura Museum, JME-ETT2 (a complete specimen preserved in lateral view), JME-ETT18 (an almost complete skeleton preserved in lateral view, showing the skull roof in dorsal view), JME-ETT88 (a partially preserved specimen, lacking the skull), JME-ETT102 (an almost complete skeleton preserved in lateral view), and JME-ETT84, JME-ETT85, and JME-ETT140 (three fragmentary specimens).

Etymology: specific name in honor to Mr. Frank Sanzenbacher who collected the holotype.

Type locality and geological age: the type locality is the stone quarry of Ettling, 50 km E-SE of Solnhofen, southern Franconian Alb, Bavaria. The age of this locality is considered as Kimmeridgian/Tithonian [20].

Diagnosis: *Aspidorhynchus* differing from all other species of the genus by at least three characters:

- the short length of the premaxillae, which project beyond the lower jaw for approximately one seventh of the total length of the skull;

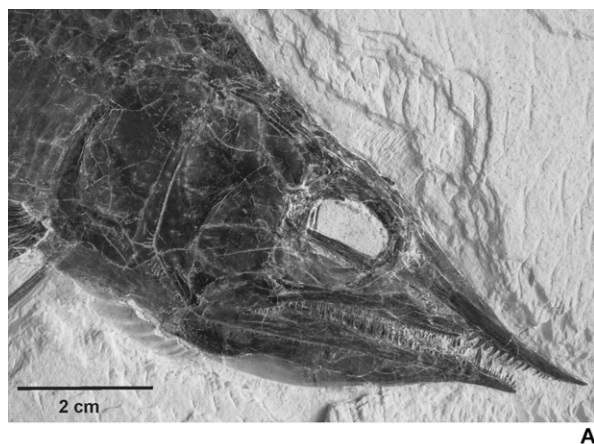
- disposition of teeth in the prementary, with a row of median large teeth, that increase in size caudally, and a row of small, lateral teeth;
- principal rays on the caudal skeleton in number of 17 or 18.

4. Description

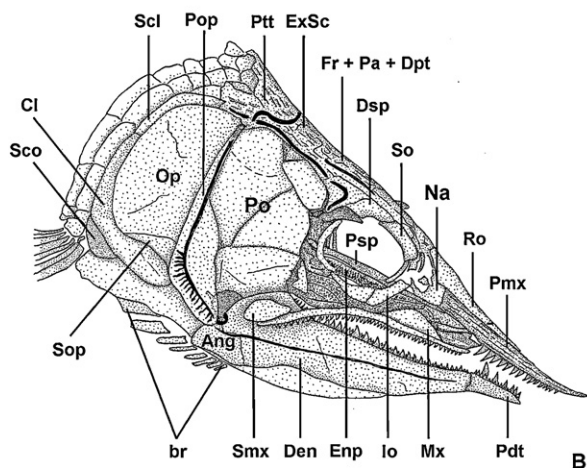
A. sanzenbacheri is known from skull and postcranial elements and is easily differentiated from the other aspidorhynchids by the short length of its rostrum (Figs. 2–5). It is a medium-sized aspidorhynchid, of approximately 305 mm long. The deepest part of the body is between the pectoral and the anal fin. The skull measures approximately one quarter of the body's length.

4.1. Skull roof

The skull roof is partially preserved in specimens, JME-ETT1, JME-ETT2, and JME-ETT18 (Figs. 2, 4, and 5). The premaxillae taper into an acute rostrum, which projects beyond the lower jaw for approximately



A



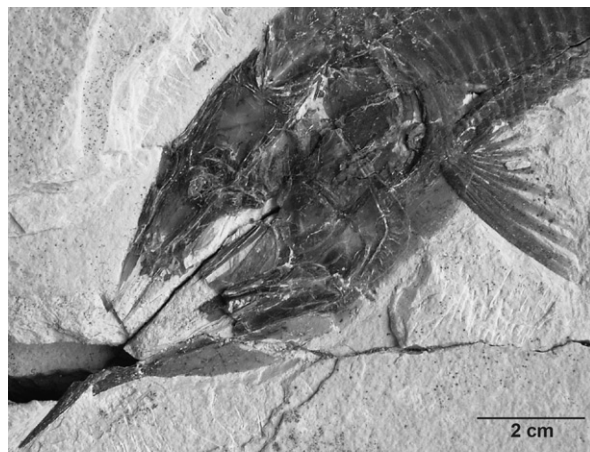
B

Fig. 4. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT2. **A.** Head in left lateral view. **B.** Drawing of **A.** Ang: angular; br: branchiostegals; Cl: cleithrum; Den: dentary; Dsp: dermosphenotic; Enp: endopterygoid; Exsc: extrascapular; Fr + Pa + Dpt: fronto-parieto-dermopterotic; Io: infraorbital; Mx: maxilla; Na: nasal; Op: opercle; Pdt: predentary; Pmx: premaxilla; Po: postorbital plates; Pop: preopercle; Psp: parasphenoid; Ptt: posttemporal; Ro: rostral; Scl: supracleithrum; Sco: scapulcoracoid; Smx: supramaxilla; So: supraorbital; Sop: subopercle.

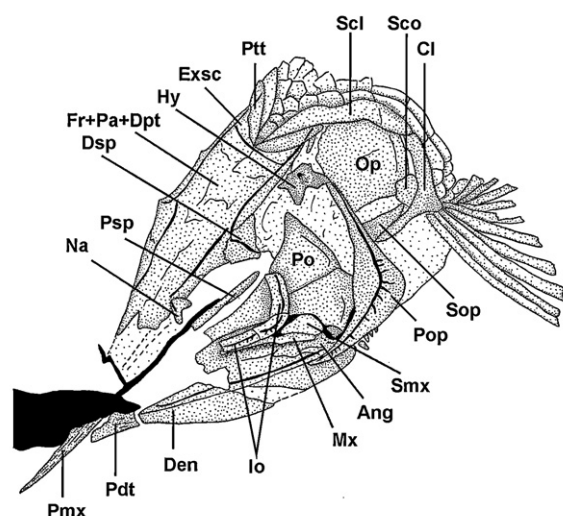
Fig. 4. *Aspidorhynchus sanzenbacheri* n. gen et sp JME-ETT2. **A.** Tête en vue latérale gauche. **B.** Dessin **A.** Ang : angulaire; br : rayon branchiostège; Cl : cleithrum; Den : dentaire; Dsp : dermosphénotique; Enp : entoptérygoïde; Exsc : extrascapulaire; Fr+Pa+Dpt : fronto-pariété-dermoptérotique; Io : infraorbitaire; Mx : maxillaire; Na : nasal; Op : opercule; Pdt : prédentaire; Pmx : prémaxillaire; Po : postorbitaires; Pop : préopercule; Psp : parasphénoïde; Ptt : post-temporal; Ro : rostral; Scl : supracleithrum; Sco : scapulcoracoïde; Smx : supra-maxillaire; So : supraorbitaire; Sop : sous-opercule.

one seventh of the total length of the skull, and are ornamented with small longitudinal striations.

The anterior extremities of the premaxillae are united along the dorsomedial line of the skull giving the impression of a single “rostrum”. The posterior part of each premaxilla is covered by the rostral, forming a kind of



A



B

Fig. 5. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT18. **A.** Head in left lateral view, showing the skull roof. **B.** Drawing of **A.** Ang: angular; Cl: cleithrum; Den: dentary; Dsp: dermosphenotic; Exsc: extrascapular; Fr + Pa + Dpt: fronto-parieto-dermopterotic; Hy: hyomandibula; Io: infraorbital; Mx: maxilla; Na: nasal; Op: opercle; Pdt: predentary; Pmx: premaxillary; Po: postorbital plates; Pop: preopercle; Psp: parasphenoid; Ptt: posttemporal; Scl: supracleithrum; Sco: scapulcoracoid; Smx: supramaxilla; Sop: subopercle.

Fig. 5. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT18. **A.** Tête en vue latérale gauche, montrant la voûte crânienne. **B.** Dessin **A.** Ang : angulaire; Cl : cleithrum; Den : dentaire; Dsp : dermosphénotique; Exsc : extrascapulaire; Fr + Pa + Dpt : fronto-pariété-dermoptérotique; Hy : hyomandibulaire; Io : infraorbitaire; Mx : maxillaire; Na : nasal; Op : opercule; Pdt : prédentaire; Pmx : pré-maxillaire; Po : postorbitaires; Pop : préopercule; Psp : parasphénoïde; Ptt : post-temporal; Scl : supracleithrum; Sco : scapulcoracoïde; Smx : supra-maxillaire; Sop : sous-opercule.

“tube” which extends, caudally into the ethmoidal region of the braincase, as in the other members of the family [8]. Each premaxilla bears a row of teeth that increases in size caudally.

The rostral bone is unpaired, deeply convex and twice as long as wide. It inserts, in front, between the posterior part of the premaxillae and caudally, overlies the anterior margin of the frontals. The ethmoidal commissure is found at the anterior third of the bone; from it, several canalicules are directed anteriorly. The ethmoidal commissure has no contact with the supraorbital canal backwards.

The frontals, as in other aspidorhynchids, are fused to the parietals and the dermopterotics during the ontogeny [8] (Figs. 4 and 5). These bones have an equal width throughout their lengths, extending from the rostral bone posteriorly to the extrascapulars. A single pair of extrascapulars is present; they are slightly longer than wide, asymmetrical, tapering medially and containing the extrascapular commissure.

The supraorbital canal finishes close to the middle point of the fronto-parieto-dermopterotic (probably in what should be the posterior margin of the frontal) and does not join the otic canal. Anteriorly, this canal goes through the nasal.

4.2. Circumorbital bones

Two remnants of infraorbitals are preserved in specimens JME-ETT2 and JME-ETT18 (Figs. 4 and 5); so we assumed that there are about three small and rectangular infraorbitals. The first infraorbital lies in ventral contact with the posterior part of the lamellar expansion of the maxilla that is located at the anterior third of the bone and joins the nasal dorsally. The posteroinferior part of the first infraorbital overlies the entopterygoid. The other infraorbitals overlie the anterior border of the postorbital bones.

The dorsal circumorbital bones are the supraorbital and the dermosphenotic. The supraorbital, forms the anterodorsal margin of the orbit contacting the dermosphenotic. Anteriorly, the lateral margin of this bone forms part of the orbital margin and dorsally it is tightly sutured to the frontal. Posteriorly it articulates with the large postorbital bone. The dermosphenotic is pierced by the infraorbital canal.

The sclerotic ring consists of two sclerotic plates.

4.3. Cheek bones

Depending on the specimen, and as described for other aspidorhynchid species [8], there are two or three large postorbital plates. They cover the anterior margin of the preopercle. The preopercle presents two well-defined parts: a vertical dorsal ramus and an expanded ventral part. The preopercular canal follows the posterior

border of the bone. There is individual variation with respect to the number of canalicules branching from the main preopercular canal (Figs. 4 and 5).

4.4. Opercular series

The opercle is hypertrophied and forms the majority of the opercular series. It is almost one and a half times deeper than long, bearing a ventral part which is more developed than the dorsal. The anterior border is straight, perpendicular to the head axis, and partially covered by the preopercle. Its posterior border is strongly convex and overlays widely the supracleithrum. The dorsal linear border is inclined ventrally at the rear, and rides over the dorsal margin of the subopercle. The triangular subopercle is reduced in size. Seven incomplete branchiostegal rays are preserved in specimen JME-ETT2.

4.5. Jaws

The upper jaw consists of the premaxilla, described above with the skull roof, maxilla and supramaxilla (Figs. 4 and 5).

The maxilla is elongated, divided into an expanded ventral part, that increases in depth posteriorly, and a somewhat rounded lamellar expansion projecting from the dorsal border at its anterior third. The oral border of the maxilla bears a row of teeth, all of similar size.

The supramaxilla is a small oval bone whose length is about one fifth of the maxillary length. It is located above the posterodorsal angle of the maxilla.

An unpaired prementary, a pair of dentaries, splenials, and angulars have been identified in the lower jaw.

The prementary is short, triangular, and toothed. It is linked to the rest of the mandible by a vertical suture. The prementary is much shorter than the premaxilla, and its length is equal to about one quarter of that of the dentary. The oral border of the prementary bears a row of median large teeth, that increase in size rearward, and a row of small, lateral teeth (Fig. 6); this disposition seems to be different from what is known in other species of *Aspidorhynchus*.

The dentary constitutes the major part of the mandible, being low at its symphysis with the prementary, and increasing in height posteriorly to form the coronoid process. The teeth of the dentary are large, increasing in size caudally. The posteriormost bone of the lower jaw is the angular. The lateral surface of this bone is ornamented with small tubercles. The mandibular canal is contained within the dentary and the angular.

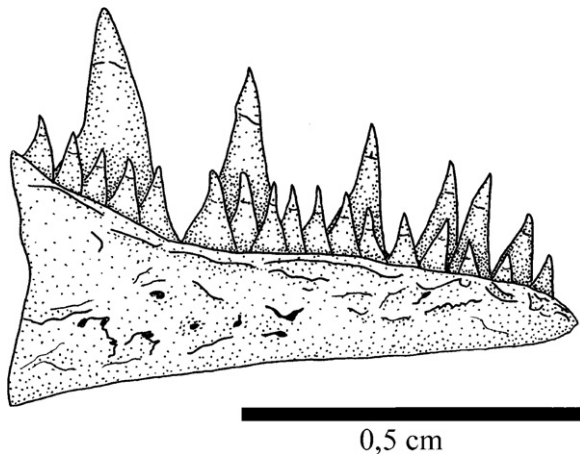


Fig. 6. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT2; detail of predentary.

Fig. 6. *Aspidorhynchus sanzenbacheri* n. gen et sp., JME-ETT2; détail du prédentaire.

4.6. Neurocranial dermal bones

Only the orbital part of the parasphenoid can be observed; it is a fragile, thin bone. The parasphenoid presents a thin shagreen of tiny teeth on its anterior part.

4.7. Palatal bones, jaw articulation, and hyoid arch

The palatal complex is not well preserved and only the ectopterygoid and the entopterygoid can be differentiated. The ectopterygoid is a thin and elongated bone, bearing an oral row of small teeth. The entopterygoid presents an internal surface with tiny villiform teeth.

The quadrate is a fan-shaped bone, lacking the posteroventral process. The bone is characterized by a thickening of its posterior border which leans against the symplectic. The ventral end of the symplectic does not reach the lower jaw, and only the quadrate is involved in the jaw articulation.

The hyomandibula is observed on specimen JME-ETT18, in where the dermal bones are displaced. The bone is stocky, being expanded and strengthened in the middle-part by a vertical rod-like ridge.

The hypohyal appears to be a single nodular element. The anterior ceratohyal is long and thin, approximately three times longer than deep. The borders of this bone are slightly concave. The bone is devoid of fenestra or groove for passage of the efferent hyoid artery.

4.8. Pectoral fin and girdle

The posttemporal bone is somewhat oval and located behind the skull; the posterior edge overlies the dorsal

end of the supracleithrum. The supracleithrum laterally overlaps the dorsal end of the cleithrum. The cleithrum has an elongated lower arm which seems to be equal or longer than the upper arm. We note a well ossified bone, similar to that found in other aspidorhynchids that is here interpreted as a scapulocoracoid (Figs. 4 and 5).

The pectoral fins are well developed and comprise eight or nine rays. The first ray is not fused with the propterygium.

4.9. Dorsal and anal fins

Both the dorsal and the anal fins are triangular and located posteriorly in the body, at the level of the 55th and 51st transversal row of scales, respectively. The dorsal fin has three unbranched and 10 branched rays. The anal fin is larger than the dorsal fin; and is formed by three unbranched and about 15 branched rays.

4.10. Caudal fin

The caudal fin of *A. sanzenbacheri* has previously been discussed and figured, but not assigned to a specific taxon [3]. The caudal fin is forked; the ventral lobe is longer than the dorsal, a character of the genus *Aspidorhynchus* among aspidorhynchids [10].

Small epaxial and hypaxial fringing fulcra are placed between the basal fulcra and the first and last principal rays.

The dorsal lobe is composed of nine basal fulcra (including the procurrent rays plus the first transverse segmented rays), and eight principal rays. The ventral lobe comprises eight basal fulcra (four procurrent rays and four transverse segmented rays) and nine principal rays.

The total number of principal rays (= 17) is lower than in other species of the genus where the caudal skeleton has been described: 19 to 22 in *A. acutirostris* and 18 in *A. antarcticus* [10,19].

4.11. Squamation

The scale rows consist of thick ganoid-type scales. The flank scales are arranged in three rows of similar size. The scales have well-developed peg and socket articulations. Dorsal to the flank scales there are three rows of small ornamented scales. The dorsalmost scale rows are ornamented by longitudinal parallel ripple-like ridges, separated by narrow intervals. Ventral to the flank scales, there are five or six rows of small, rectangular, smooth scales.

As in the other species of the genus [11,23], the histology of the scales showed the complete absence of ganoin in *A. sanzenbacheri*.

5. Taxonomic affinities and conclusions

Although a phylogenetic revision of the family Aspidorhynchidae is in progress, *A. sanzenbacheri* shows the synapomorphies of the family, including: the presence of a “rostrum” composed by the premaxillae; presence of a predentary; posterior position of the preopercular canal; and absence of interopercle.

Within Aspidorhynchidae, *A. sanzenbacheri* is assigned to the genus *Aspidorhynchus* as it possesses the following characters: three rows of flank scales of approximately similar size; absence of a ganoine layer on the outer surface of the scales; and a caudal fin with a ventral lobe longer than the dorsal lobe.

The combination of the following characters confirms this taxonomic position: presence of a short predentary. This feature is found in *Aspidorhynchus* but also in *Vinctifer* and in an indeterminate Cretaceous taxon from Chile [4]. However, in *Vinctifer* the teeth are small while in the Chilean form this bone is edentulous. In *Belonostomus* the predentary is long being subequal or almost equal in length to the premaxilla.

A toothed premaxilla, a maxilla divided into an expanded ventral part with a rounded lamellar expansion, and a posterior small supramaxilla. These three characters are shared with the genus *Belonostomus*, but not with *Vinctifer*. In *Vinctifer* the premaxilla is edentulous or has a row of very small and tiny teeth. On the other hand, *Vinctifer* has a maxilla divided into an anterior elongate ramus lying parallel to the premaxilla and a plate-like posterodorsal border [7,8]; due to the posterior prolongation of the maxilla, this taxon lacks a supramaxilla.

The following combination of features appears to be unique to *A. sanzenbacheri* among the genus *Aspidorhynchus*. Firstly, premaxilla projects beyond the lower jaw for approximately one seventh of the total length of the skull (*versus* one third in *A. acutirostris*, *A. spekodensis*, *A. fisheri*, and *A. crassus*; one quarter in *A. euodus*; one half in *A. arawaki* and unknown in *A. antarcticus*). Secondly, predentary bears a row of large, medial teeth, increasing in size caudally, with a row of small lateral teeth; and eventually, 17 principal rays on the caudal skeleton (*versus* 19 to 21 in *A. acutirostris*, 18 in *A. antarcticus*, and unknown in the other species).

Further phylogenetic study of the genus will clarify the relationships within this genus, as well as between this genus and the other aspidorhynchids.

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